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THE BOTANICAL REVIEW

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THE CUTICLE IN ANGIOSPERMS

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INTRODUCTION

Like most words in common use, the term "cuticle" has been employed in different senses, even in botanical literature. In these pages it is applied to the surface layer of the epidermal wall in shoots of herbaceous phanerogams, which has characteristic, fatty properties. Such a layer is widely distributed among plants, but there is some evidence that it is frequently absent from or very poorly developed in ferns (21). Intensive study of recent years has been practically confined to the very well developed layer in angiosperms, so that this review deals only with the angiosperm cuticle. Its consideration necessarily leads to some examination of the wall structure of the epidermis, for the cuticle forms the outermost layer of the outer epidermal wall. In this review the cuticle is the focus of interest; heretofore it has received only incidental treatment in *THE BOTANICAL REVIEW*, in a paper dealing with wall structure in higher plants (4).

The nature and development of the cuticle has been previously discussed by the present writer (21) from a standpoint which has been challenged on occasion but which at least provides a starting point around which to orient recent contributions to our knowledge of the layer.

The nature of the cuticle proper can thus be examined, but probably the main advance of the last two decades has been due to use of the polarising microscope, which has firmly established the concept of layered construction of the outer epidermal wall. A review of this work follows.

The layered construction of the epidermal wall is naturally much clearer where the wall is thick, and the work has so far been based upon very few species. It seems to receive further elucidation and to contribute to a more general understanding of cuticular organisa-

tion when reviewed in the light of tissue development, so that some estimate may be made of the effect of the method of cell growth and cell division upon formation of the epidermal wall of which the cuticle is so conspicuous a feature.

In angiosperms the cuticle distinguishes the shoot from the root. In any developing dicotyledonous seedling, when close attention is paid to the region of transition, the shiny surface of the shoot, at the base of the hypocotyl, merges rather sharply into the dull surface of the root. A drop of water on the surface of the shoot does not display any tendency to spread, but on the root it immediately spreads, and if the root be horizontal and small and the drop large, the latter accumulates on the lower side. Thus the characteristic, fatty, non-wettable nature of the shoot cuticle is demonstrated.

It was argued previously that the cuticle is to be attributed to accumulation on the surface of the growing shoot, of fatty substance released from the living protoplasts within; but the root is likewise a growing system, and the question arises why there is not a similar accumulation of fatty substances there. A cuticle covers the embryonic radicle and may also be found occasionally on slowly growing roots (21), but the different organisation of the growing root apex provides a complete explanation of the absence of a cuticle as a normal structural feature. It is an invariable consequence of this method of apical organisation that the surface layer of the root, the protoderm, differentiating later into the piliferous layer, continually slides out from beneath the tissue of the enveloping root cap. As a consequence, it rubs its future external surface against the inner surface of the cells of the root cap, and the most superficial examination shows that this process is associated with release of relatively large quantities of pectic substances. With these, any fatty substances tending to accumulate on the surface of the protoderm, will be carried away, and by the time this layer is free from the root cap, apparently the most lively release of fatty substances to the exterior is already over for these tissues (8). Fats from cells deeper within accumulate in the Casparian strip of the endodermis; later, fatty substances may accumulate on the inner surface of the cells of the hypodermal layer which then forms the exodermis, but usually no distinct fatty cuticle is found over the surface of the root. At the growing apex of the shoot no sliding of layers over one another removes the accumulating fats, and from

the very beginning this surface is covered with a cuticle. Too thin to prove any hindrance to cell growth and form changes in these early stages, it rapidly thickens and changes in its physical nature until even in the still growing plant its proportions and properties must be given serious consideration as factors possibly limiting volume expansion and moulding form.

THE CUTICLE PROPER

The summit of the growing shoot apex is always a group of actively dividing, meristematic cells, all very much alike. Among them the dermatogen is usually distinguished as the outermost layer but cannot be separated in any other way than by its position which is maintained by the fact that cell divisions are exclusively in the anti-clinal direction. Cell divisions are anti-clinal also in one or more layers of underlying periblem, and these layers are now often grouped together as the "tunica" as distinct from a deeper lying "corpus" in which cell divisions occur in all planes (12).

From the outset the essential first stage of a cuticle is present over the apex as a continuous layer of fatty substances overlying the cellulose walls of the outermost cells. If the cellulose walls are swollen with zinc chloride or 70% sulphuric acid, this fat layer may separate from the walls beneath and can be traced as a continuous layer, staining yellow in iodine reagents, and quite free from any trace of a cellulose reaction.

If, then, the fatty substances are to be regarded as secreted, or excreted, from living cells within, there can be no reason to ascribe their excretion in this region exclusively to the dermatogen layer. Later, when the cells of the dermatogen are more fully differentiated, their protoplasts show obvious differences from those of the underlying cortical cells and their metabolism may well be different, but there seems little reason to assign to any cells of the meristematic apex a preponderating rôle in a metabolic activity which releases fatty substances from the protoplasts into the walls. Thus substances such as glycerides of fatty acids and waxes—esters of fatty acids with high molecular alcohols (39)—are released into walls which in this growing region are saturated with water, and these fatty substances, made up in part of long hydrocarbon chains without affinity for water, certainly tend to migrate to the nearest air-water surface where they accumulate with their hydroxyl or ester

groups in the water surface and their hydrocarbon chains in the air. The fatty acids in these substances include, as do all vegetable fats, unsaturated linkages, and these in the air oxidise and thus gradually link up together with elimination of water from the molecule. Thus, from a continuous film of oil or fat, originally covering the surface of the plant, a film of more varnish-like consistency gradually forms. Such changes in the fatty constituents of growing points have been followed in the laboratory (42). As certainly as a vegetable oil spread over a picture oxidises and "dries" to varnish, so do these oil surfaces spread over any air-water surface on the growing shoot. This means that the apex is covered by a continuous film of "drying" fat in which oxyacids and waxes are present in varying proportions. This general statement of the causes underlying production of the plant cuticle seems to have met with general assent since first put forward, but it may be reexamined in the light of some criticisms. In a series of papers, Thoday and his colleagues have insisted upon the functional differentiation that is present in what might be superficially regarded as uniform parenchymatous tissues. By micro-chemical methods, most striking examples of such heterogeneity of metabolic function have been established. In a general presentation of this work (49), Thoday examines the above argument as to the origin of the cuticle. His data certainly show that an epidermal layer may well be expected to display metabolic specialisation, either as a result of special origin—by continuous anticlinal divisions—or of special position, and that this specialisation may include secretion of the cuticle. But the cases which he cites in support of this position seem actually to lead to the opposite conclusion. He cites first the work of Damm (7) on the structure of dicotyledonous epidermal structures lasting many years. Damm describes most fully the epidermis of *Viscum album* where not merely in association with cracks in the epidermis, as Thoday's account would suggest, but all over the stem, cuticular layers, that is, layers of cellulose impregnated with fatty substance, accumulate not only outside the epidermis but inside the epidermal cells as well. Such layers are obviously the result of release of fatty substance from the cells within the epidermis; they are evidence of this and are so regarded by Damm.

As the result of this continued accumulation of cutinised layers within, first the epidermal cells and then the outer cells of the cortex

are gradually cut off from the living tissue within, undergo post-mortem changes and lie embedded as dead cells in the mass of cutinised wall layers. Damm proposed for the whole thickness of cutinised layers with the embedded cells, the term "cuticular epithelium". In view of the use of epithelium for the living and actively secretory cells lining various secretory canals, the choice of this term does not seem very appropriate, nor can it be regarded as a convincing argument for the conclusion that the fatty secretions in the cutinised layers arise from the embedded cells. It is clear that after being thus embedded these cells cease all vital activity and merely provide evidence that at least cells within the innermost layers thus embedded probably contribute to the release of fatty substances, a conclusion which is implicit in Damm's own statement of his observations.

Thoday's other and clearer case is provided by the collenchyma in the outer layer of the base of the connate perianth cup in the fruit of *Arceuthobium pusillum* (50). This tissue is several cells deep and practically without air spaces; its walls, like cutinised membranes, give no cellulose reactions until treated by alkalis or fat solvents to remove the impregnating materials. This impregnating material is more readily soluble in cold potash, in the material examined by Thoday and Johnson, than is usual in typical cutinised lamellae; furthermore, complete disappearance of these wall layers in boiling potash suggests that the basal substance is mainly, if not entirely, of pectic nature, so that it would seem inadvisable at present to use the same terminology for them as for the cutinised layers of the outer epidermal wall. They do provide, however, clear evidence of fat deposits which are most probably due to the secretory activity of the developing collenchyma itself.

But this argument surely simply implies that this tissue, as probably every other developing tissue of the plant, normally releases fatty substances during development. The exceptional fact is that these substances are in this case retained in the walls instead of being released to the surface of the plant and appearing in the cuticle. Incidentally, the cuticle in this plant is prominently developed, and there is evidence from staining reactions for a very general impregnation of the walls of all tissues with fatty substances. Where there is such accumulation of fat it is not surprising that in a closely packed collenchyma with gelatinous walls, much of the fatty deposit never succeeds in migrating to the outer surface.

Scattered throughout the literature is a very general recognition that in closely packed tissues, such as sclerenchyma and collenchyma, the outer walls of the individual cells usually retain material quantities of fatty substances. This is not readily recognised by the microchemical reaction of the walls as seen in section, though it may be suggested by the difficulty with which such walls yield cellulose reactions until after vigorous pretreatment with fat solvents, but it is frequently suggested by observations upon the walls of the elements of these tissues after isolation by maceration processes. The botanist frequently uses the violent maceration agent of Schulze after which almost all wall reactions save for cellulose have disappeared, but if milder reagents are used, then the more resistant nature of the outer lamellae to cellulose solvents or to swelling agents is usually noted. A recent paper draws attention to this characteristic of collenchyma cells in *Heracleum* (23); these observations were carried out in the writer's laboratory, and the fatty nature of the outermost layer of the fibres macerated in chromic acid was very definitely suggested by the yellow colour of this layer in such reagents as zinc chloride and iodine. As the point was not directly under investigation, however, no definite conclusion was drawn by the authors as to the nature of the outer deposit.

Sclerenchyma fibres are often utilised in industry, and in this case the strands of fibres are isolated by relatively mild macerating agencies. As a result, the technical literature of such fibres is littered with incidental references to the fatty nature of some of the wall substances, and the fibres are frequently spoken of as possessing a cuticle, the chemical nature of the "cutin" being reported upon as the result of manipulations upon extracted materials which, however, may not necessarily all be derived from an outer cuticular layer (16, 18, 11, 19, 48). Evidently when these fibre strands are isolated from the plant by mild maceration, the considerable quantities of fatty substances in the walls, as a result of exposure to the air, may well undergo the usual "drying" changes, so that in the course of time the technologist deals with a fibre possessing an outer layer which has at least some of the characters normally attributed to the cuticle.

But actually this argument, arising out of Thoday's observations upon a very specialised tissue and type, admits of the widest exten-

sion. Consideration of the literature shows that there is much evidence that most if not all tissues of the living plant tend to release fatty substances from the living protoplasts during development, that these fatty substances appear in the walls, and that if the walls form a continuous system, not directly exposed to air, the substances may move along them to other regions, but that in any tissue, if such fats are long exposed to air, they tend to be deposited in the tissue with the resultant formation of a cuticle-like deposit on the outer surface of the wall which is in contact with the air. Ursprung's (51) experiments, in which leaves were torn so as to expose unbroken walls of the internal tissues and these tissues then dipped under a water surface bearing a layer of lycopodium spores, talc or charcoal, showed that such walls frequently gave evidence of the release of surface active substances, bringing about a rapid removal of the film of fine powder from the neighbourhood of the immersed tissue. In many cases he supplied further evidence that this surface deposit on internal cellulose walls, which prevented ready movement of water along the intercellular space system, could be removed by fat solvents. Arzt (6), on the basis of widespread investigations, concluded that an inner cuticle, that is, a continuous though thin layer of deposit staining with fatty solvents, was widespread, perhaps general, in leaves of dicotyledons. He argues that if his conclusion is confirmed there is no need to ascribe a polar character to cuticle secretion and regard it as an externally directed secretory property limited to epidermal cells. Whenever cells are in contact with air and not with each other we may expect such a deposit, though frequently its recognition provides considerable difficulty. Gêneau de Lamarlière (15), in his studies of water plants, also established the general presence of an internal cuticle lining the well developed intercellular space system.

Frey-Wyssling and Elsa Hausermann (13a) have extended Ursprung's observations on the difficulty of wetting the cell surfaces bounding the intercellular spaces in the leaf and conclude that lipophil deposits must be present and that, in view of the fact that they resist extraction in wax solvents, these substances must be definitely of a cuticular nature.

One characteristic of the cuticular layer evidently associated with its production by accumulation of migrating fatty substances to the external surface of the cellulose layers, is that while the cellulose

layers generally show in their lamellation and organisation evidence of formation by the protoplasts within, the cuticular layer lies smoothly over the whole intricate pattern of epidermal tissue and has usually a uniform thickness throughout its extent. When released by swelling agents, however, the pattern of the anticlinal walls may show on it owing to release with it of inwardly projecting ridges of fatty substances that accumulate in the middle lamella regions. These fatty substances migrate into the cuticle over a long period of the plant's life; thus the cuticle may continue to grow in thickness, though, on the other hand, as these substances are fairly mobile in water they may be leached away as fast as they are produced.

The presence of such surface active substances escaping from a normal leaf surface may be revealed by touching clean water or mercury surfaces with uninjured leaves, when a fine talc powder shaken on the surface is carried rapidly away from the point in contact with the leaf. Devaux (8) concluded that from young leaves the substances diffusing were mainly lipoidal and contributed to the unwettability of the leaf; in older leaves they become more hygrophilous colloids and so the adult leaf surface is more wettable.

The fact that these fatty substances fuse into a continuous sheet which overlies all epidermal cells and shows little or no relation to individual cells is evidence again that this layer may well receive contributions from all underlying protoplasts that release fatty substances, provided they migrate. There can be no doubt about this communal nature of the fatty layer. It is confirmed by consideration of cases like the ovule, where when two originally independent surfaces become closely pressed together in growth, the cuticles, originally separate, fuse into a common layer. Thus the cuticle on the inner surface of the inner integument fuses with that over the surface of the nucellus, and there is only one common cuticle finally between inner and outer integuments (37). A still more striking case is the fusion of the cuticle into a common layer where the petals are in contact over the flower bud in *Ligustrum vulgare*; a similar phenomenon is reported in *Hedera Helix* (47).

CUTICLE AND CUTICULAR LAYERS

Probably in every case the outer epidermal wall is relatively complex in nature and shows gradation, usually from a pure cellu-

lose wall, facing the epidermal protoplast, though layers containing varying quantities of pectic substances and fatty substances to an outermost sheet of cuticle free from cellulose and usually free from pectin compounds owing to the leaching action of the weather on these relatively soluble substances. In most plants the thickness of the wall is not great, and this structural complexity is not easily analysed—that is why almost all modern work on which our views as to the nature of this complex organisation are based, has been carried out on a relatively few plants, *e.g.*, *Clivia nobilis*, *Aloe*, *Gasteria*, *Dasyllirion*, *Aucuba*, in which the outer epidermal wall is exceptionally thick. This must be borne in mind when there is a tendency to generalise statements on sub-cuticular organisation; it may not be without significance, for instance, that most recent work has been carried out on monocotyledons.

While very thorough studies have been made of some of these thick epidermal walls by micro-chemical methods (38, 14), these recent advances have depended in part upon the polarising microscope.

So long ago as 1888 Ambrohn (1) confirmed an earlier observation of Dippel that the anisotropic qualities of cutinised and suberised membranes disappeared on treatment with alkali. Removal of impregnating substance by this means left the membrane either neutral in refractive properties or showing the reverse optical refraction typically characteristic of cellulose. Ambrohn further noted that if the sections of leaf epidermis of *Clivia nobilis* or of birch cork were warmed to 100° C. in water or dilute glycerine, the impregnating substances in the cuticularised or suberised walls melted and the double refraction disappeared, to reappear again in cooling; throughout this manipulation the optical refraction of the neighbouring cellulose walls remained unchanged.

Little further advance was made in our knowledge of the complexity of the cuticularised epidermal wall until its further exploration with the polarising microscope (13, 2, 3, 36). It is now clear that there are various lamellae of different composition oriented parallel to the surface in such a wall and that these lamellae are also interrupted in some way in regions that lie over the anticlinal walls of the epidermal cells; over the whole of the complex structure lies the smooth, uninterrupted sheet of cuticle. Immediately within the cuticle are layers, more or less distinct, having a matrix

of cellulose characterised by varying degrees of impregnation with fatty substances, which can be removed only by most thorough and prolonged treatment with saponifying or oxidising agents. These cutinised lamellae have a negative double refraction varying in degree throughout the layers, a gradation that depends upon the amount of impregnating substance responsible. This is probably crystalline with a comparatively low M.P., as all later work has confirmed Ambronn's observation of the disappearance of this negative refraction with rise of temperature and its reappearance on cooling. The double refraction is termed negative in the sense in which the term is used by Frey-Wyssling (33), and the higher refractive index is in a plane at right angles to the direction of the carbon chains of the cellulose molecules in the wall, these carbon chains lying parallel with the long axis of the cellulose micelles. The higher refractive index of the cellulose wall alone is in a plane parallel to the axis of the cellulose micelles, and this is spoken of as a positive double refraction.

In the cutinised lamellae the negative double refraction masks the normal positive double refraction of the cellulose, and in the outermost lamellae the cellulose may be so widely dispersed, among pectin and fatty substances presumably, that, for instance in *Clivia nobilis*, little indication of any double refraction remains after the fatty substances are completely removed. When examined under crossed Nicols, a wall region is usually found within the outer area of negative double refraction showing the normal pronounced positive double refraction of cellulose. In *Yucca* no positive inner layer is seen, and in *Dasyllirion* it is only faintly visible. Micro-chemical tests show that in these walls impregnation with fatty substances (the cutinised lamellae) persists practically throughout the full extent of the epidermal wall. In *Clivia*, *Gasteria* and *Aucuba* this inner positively refractive region is very marked and constitutes a striking feature in a region which appears completely isotropic, lying between these lamellae with opposed refractive properties. In this zone pectin appears to preponderate, but careful swelling of the walls and treatment with pectic stains, while confirming the appearance of this very marked pectin lamella, also suggests further stratification into numerous lamellae of varying pectin content (14).

This stratified appearance of the outer epidermal wall thus suggests a wall in which fatty substances migrate outwards. At the

surface they coalesce to form the continuous isotropic layer of cuticle, but within they remain dispersed in a series of lamellae characterised by varying relative proportions of cellulose and pectin.

Among these "fatty" substances we must distinguish between a solid wax, readily melted and extracted by fat solvents, and a non-meltable substance extracted only by prolonged treatment with hot alkali or strong oxidising agents, the "cutin", probably composed mainly of oxy-fatty acid products formed from migrating, unsaturated, fatty substances after exposure to air. The wax is responsible for the negative double refraction (36), but Küster's observations upon sphaerites of cutin in *Gasteria* (36) suggest that the wax molecules themselves have the strongest refraction parallel to the molecular axis.

But the negative double refraction is produced only by the solid wax, and probably the wax, like paraffin, crystallises into platelets in which the molecular axis is at right angles to the surface of the plate. Such platelets would most naturally lie periclinally in the cellulose wall and thus give the whole lamella the strongest refractive properties in a direction at right angles to the cellulose micelle, thus masking with this negative double refraction the ordinary positive refraction of the cellulose. This would be the natural position for such solid platelets to assume in the lamellated wall, and their swelling and recrystallisation in the same position would explain both the negative double refraction of the wall when seen in section in any plane and its disappearance with rise of temperature and reappearance on cooling. The "cutin" material is isotropic but is responsible for the strong absorption of ultraviolet radiation by these cutinised lamellae.

These substances would seem to migrate outwards through a matrix of layered cellulose and pectin which is continually added within as long as the wall continues to grow in thickness. Naturally, therefore, in most epidermal walls it is possible to detect within the cutinised lamellae a layer which either gives immediately the cellulose reaction with iodine and potassium iodide and hydrolysing agents or will give it after very brief treatment with alkali or fat solvents.

The strong tangential lamellation of the cutinised layers (strikingly figured by Linsbauer in the leaf epidermis of *Eucalyptus* (22)) and of alternating layers with varying proportions of cellu-

lose and pectin, together with the occasional occurrence of a single isotropic, predominantly pectin, lamella, may receive some elucidation if tissue development is considered. At the same time an explanation immediately appears of the point to which attention was drawn by Frey-Wyssling (13), that while the cuticle proper is continuous over the whole epidermal surface, these other lamellae show discontinuity over the region of the anticlinal epidermal walls. No feature is more characteristic of the angiosperm epidermis than its continued growth by cell divisions which, though they may lie in and between the transverse and radial planes, are never tangential, *i.e.*, they are always anticlinal, never periclinal. Any epidermal structure is the final result of such divisions, and if wall thickening is not delayed until the very last division, then a consideration of cell division (41) will show that the lamellation of the outer epidermal wall must reflect in part the succession of parent walls within which new cells arise by protoplast subdivision, followed by formation of a new wall, interior to all earlier wall lamellae and continuous around each new daughter protoplast. If wall thickening starts very late relative to cell division, then the parent wall will be thrust far to the outside of the outer epidermal wall and all the inner part of the wall will be formed only of the wall of the last formed cell because, after cell division, the cellulose content of the original parent wall undergoes no further increase, the original cellulose layer may be stretched to a breaking point or the cellulose more widely dispersed amongst pectin and fatty substances capable of migrating outwards as they are released by the protoplast. In that case all these inner lamellae, forming the major bulk of the wall, will not be continuous over any anticlinal wall but will run inwards into the anticlinal wall as they are formed separately around each individual protoplast. The general nature of the lamellation, interrupted at every anticlinal wall, as suggested for *Aucuba* and *Clivia* (13), for *Dasyliirion* and *Yucca* (36) and for *Eucalyptus* (22), suggests that this is the normal method of growth of the epidermal layer. But in the outer cutinised lamellae there are probably thin, very stretched layers in which the cellulose is widely dispersed, which have cracked completely in the regions over the anticlinal walls because as the inner walls thicken and the cells of the epidermis undergo their final expansion, the strain on the original parent walls must be very great. Such an origin of these

outermost cutinised lamellae, as much stretched lamellae deposited in succession at the surface of protoplasts undergoing alternating phases of growth and cell division, would not only explain their relative paucity in cellulose, widely dispersed among fatty and pectin materials continuing to accumulate within them, but might also help to explain the fact that the fatty materials make but slow progress outwards through such separately deposited and relatively discontinuous lamellae and thus have time to become very completely oxidised and "embedded" in each lamella. Hence, the persistent nature of fat impregnation in these cutinised lamellae and the difficulty in its removal which often needs treatment over weeks with strong alkalis and oxidising agents, often at relatively high temperatures.

In transverse divisions giving rise to longitudinal files of cells, so characteristic of the cortex of the short internode in angiosperms, the parenchyma cells divide during wall thickening, and, as a result, at one stage of growth files of cells of common parentage can be distinguished, since they remain for a time surrounded by common wall layers. In this case the longitudinal walls show no difference in thickness, but, since successive divisions are transverse, the transverse walls vary in thickness, being thinner where they separate the most recently separated protoplasts than when they intervene between cells separated at an earlier division where these transverse walls are made up not only of the thickness of the wall around the last formed protoplast but also of one or more thicknesses of earlier parent walls. At a later stage in differentiation all the cells of the file increase considerably in size without further cell division, stretching these original cells considerably, while an inner wall lamella of uniform and much greater thickness is laid down within, so that usually the original difference of thickness on the transverse walls due to this series of divisions, is no longer recognisable.

In the epidermis all divisions are anticlinal, and the parent walls, as seen in transverse or longitudinal section, may reveal at some stage in development a difference in thickness indicating the immediate parentage of the groups of epidermal cells. Nevertheless with final increase in size and increased deposit on the inner wall of every cell, this original distinction in thickness and prominence of certain anticlinal walls may no longer be visible. Such a figure as

that given by Öztig for *Psammophora longifolia* (38, Fig. 9d) suggests such groups of cells of common parentage separated by parent walls sufficiently thickened and externally cutinised to remain distinct after the last few divisions; and in *Clivia miniata* in longitudinal sections of the leaf—in which nearly all cell divisions are transverse—the last one or two transverse cell divisions may be recognised by the lesser degree of, or complete absence of, inwardly projecting cutinisation over the anticlinal division wall. Usually such distinctions in anticlinal walls cannot be recognised, and most of the thickness of all the wall of each epidermal cell, including the outer wall, must be ascribed to the activity of the existing isolated protoplasts. No outer parent wall can be detected running uninterruptedly over the anticlinal cross walls associated with more recent divisions. Naturally, therefore, with increasing expansion of the shoot and increasing thickness of the outer wall around each protoplast and not over the anticlinal partition, there will be a tendency for these epidermal walls to round off from each other and to separate along the anticlinal line, but into each such place the impregnating substances will be ready to migrate moving all the time to the surface. Thus there accumulates, not only at the surface as cuticle but over the anticlinal walls and even in some cases between the epidermal cells, the internal cuticular “ribs” (“kutinisierte Leisten”) which form such a characteristic feature in sections of these thick epidermal walls (see particularly 14 and 38). It is in accordance with this view of their development that observation shows these characteristic wedge-shaped internal ribs to be relatively late in development. In a section of the petiole of *Aucuba* one-third grown, they are not present, but are well developed in the fully grown petiole. Similarly, in an adult leaf of *Gasteria* they are fully developed at the distal end but are not present in well developed epidermal cells at the growing base of the same leaf. In *Gasteria* the adult epidermal cell develops a number of peg-like ingrowths from the outer cutinised lamellae which project inwards into the inner cellulose layers. They are also well developed in many species of *Aloe*, and Fritz (14) speaks of them as the result of an anticlinal infiltration of the cutinised lamellae into the layer within. These again are relatively late in development and may well be the result of further disintegration of the overstretched original cellulose lamellae and accumulation of impregnating sub-

stances in the cracks then produced. In some cases, as Fritz particularly notes, the internal cutinised ribs over the anticlinal walls seem separated from the superficial cuticle, but close micro-chemical examination will probably show that the outer cellulose layers are usually interrupted over the anticlinal walls and that where the cuticle thus seems separated from the internal cutinised rib, this is brought about by an accumulation of pectin or other impregnating substance, not by cellulose.

Where the proportions of fat-impregnating material seems small compared with other material accumulating in the outer layers, the cutinised region, instead of spreading throughout the whole subcuticular surface, may be restricted to a lens-like or peg-like development in the centre of each epidermal cell (38). More rarely such central cutin pegs may be associated also with cutinised anticlinal ribs.

These localised distributions of cutin deposits are reported particularly for the Mesembryanthemeae and are probably not unconnected with the frequent and considerable accumulation of crystals of calcium oxalate in the same walls. Thus in *Lithops lateritia* and *L. Lesliei* a central lens or peg of cutin is surrounded by a zone of wall densely filled with crystals (38, Figs. 4a & 4c).

Distribution of the impregnating substances in the epidermal wall naturally raises questions as to the channels by which they migrate to their positions. From time to time observations have been recorded that suggest special channels rather than general diffusion through the carbohydrate materials forming the wall basis. In particular, Dous (9), observing wax-secreting leaf surfaces by reflected light, has figured release of such excretions in *Primula Kewensis* as threads emerging from pores; in *Agave* Dous saw the pores and assumed a similar method of excretion. Ziegenspeck (54) appears to have been encouraged by these observations to re-interpret the fine anticlinal lines often noted in the thick epidermal walls of *Aloe* as fine pores facilitating fat and wax excretions. Fritz (14) gave these fine markings very thorough examination. They were seen best in material macerated by bacterial action and then stained with either Sudan III or aniline blue. He ascribes them to the original heterogeneity of the cellulose basis of the cutinised layers and points out that in many cases, although they penetrate far to the interior of the wall, they are bordered within by

a continuous cellulose membrane. This is only a more recent phase in a long debated problem, but at present, apart from such special cases as figured by Dous, the evidence would suggest that the optical properties of the cutinised lamellae are due to the presence of sub-microscopic crystalline platelets of wax, lying parallel with the surface and thus in conformity with the long axis of the cellulose micelles, and that these wax molecules reach their positions by diffusing through sub-microscopic intermicellar channels. Some evidence for sub-microscopic channels, permitting movements of salts through the wall more readily perhaps in certain regions than in others, has been provided recently by a fluorescence technique (43).

THE SURFACE PATTERN OF THE CUTICLE

The researches of Martens, in particular, have shown how much light may be thrown on the nature and significance of the cuticle by a study of its surface appearance at various stages of development. His observations began with a particularly suitable object, the wilted petal of *Tradescantia virginica*, where the cuticle of the lower epidermis readily separates from the epidermal wall, thus permitting study of the surface of the isolated cuticle (27, 28). A method for photo-micrographically recording the relief on cuticle surface at various stages of development was then elaborated, and development of the cuticular pattern followed in the petals of a number of species (29-32). As a rule, the cuticular surface in early stages is quite smooth and of uniform thickness but later may develop a pattern of folds which change progressively during cell growth and extension. While these folds obviously represent an increase in accumulation of cuticular material, Martens concludes that the cuticle proper still remains of uniform thickness and that the relief pattern is due to projecting folds of this uniform envelope, the lower surfaces of each fold adhering closely together. Initial development of such folds is difficult to follow; but it would seem to involve gradual crinkling of a cuticular envelope free to move on an epidermal wall surface undergoing repeated slight adjustments in area; frequent slight changes in volume of the epidermal cells, with varying water content, are obviously to be expected. That the cuticle itself should readily slip upon the wall beneath is perhaps supported by Martens observations upon the relations between the cuticle and the underlying wall in the staminal hairs of *Tradescantia*

(25, 26). As the flowers wilt, a violet coloured sap usually accumulates at the base of the flower, exosmosing from the petals. The staminal hairs bathed in this fluid often show ready separation of the cuticle from the underlying walls. There is still argument as to whether this separated outer layer is pure cuticle or cuticle plus some cutinised lamellae (52, 33, 34), but in either case separation from the cellulose-containing inner wall seems due to hydrolysis, under the special conditions, of an intermediate lamella composed principally of pectic substances. If, then, the cuticular layer can slip upon the cellulose wall beneath, and if this cellulose wall undergoes frequent slight fluctuations in surface apart from any steady increase in surface due to growth, wrinkles in the cuticular envelope may be expected, and such wrinkles, adhering together by their inner surfaces now separated from the cellulose layer beneath, are Martens interpretations of the relief pattern in the cuticle. In many cases these folds form at first simply an irregular reticulate pattern as cells beneath them increase in volume. Then, if the increase is greater in one direction than another, in the direction of major extension, such folds will once more be smoothed out as an increased cuticular surface is required to cover the increased epidermal area.

Thus in a cell that is longitudinally stretched with little transverse expansion, an original cuticular network will be converted into a series of longitudinal folds, all folds oblique or transverse to the main axis of extension being obliterated. The pattern of cuticular folds around a central papilla, where such is present in each epidermal cell, and which usually radiate from the base of the papilla, receives a similar explanation. In these conclusions, which seem thoroughly substantiated, we see evidence for a passive stretching of the cuticular envelope during expansion of the vacuolating epidermal cells. The experiments carried out upon staminal hairs supply striking evidence that the cuticle may provide considerable resistance to such cell expansion and that if the cuticular envelope be broken while the cell contents still retain their tendency to expand, the inner walls of the cell may stretch very considerably and very rapidly.

THE FUNCTION OF THE CUTICLE

The cuticle has been regarded in these pages as the more or less inevitable result of accumulation of unsaturated fatty substances re-

leased during cell metabolism at the outer air-water surface of plant shoots. To such a layer there need not be ascribed a function as a teleological necessity to explain its presence. None the less, gradual accumulation of such a fatty layer, especially as it increases in thickness and solidity, must profoundly influence many processes in the living plant. It is a very interesting fact that the different courses taken by differentiation in root and shoot lead in the one case to fat accumulation in the Casparian strip of the endodermis where it plays an important part in the mechanism of water absorption (46), and in the other to a superficial cuticular deposit which can not be without influence on water retention. The first and obvious suggestion as to cuticular functions in the shoot has always been that it contributes to control of water loss, and from very early days attempts have been made to evaluate the comparative significance of cuticular and stomatal transpiration. The prevalence of thick cuticles in plants of xerophytic situation seems support for this interpretation, but again recent papers have drawn attention to the frequency with which thin cuticles occur in such situations. Strongly thickened epidermal and hypodermal walls are more characteristic of the Bromeliaceae and of many other plants with well developed succulence having their water storage tissues covered by a comparatively thin cuticular envelope (35). On the other hand, thick cuticles are well represented in plants of the peat bog (40), and these plants, when well supplied with water, show a comparatively high rate of water loss per unit surface.

Kamp (17), too, has submitted the question of relation between cuticle thickness and cuticular transpiration to close analysis, to show once more that the cuticle is only one of many factors influencing transpiration and that, in general, it is by no means the most important; also, that only in a comparison between closely allied plants is it possible to find any inverse correlation between cuticular transpiration and cuticle thickness. In view of Anderson's observations that cutin is impenetrable to ultra-violet radiation (2), Kamp suggests, however, that the thickness of the cuticle may have other much more general significance than an effect upon transpiration.

While, then, the general result of a large body of work is to deprecate any hasty conclusion that cuticular thickness has a preponderating rôle to play in controlling water loss, there is a most

curious conflict of evidence at present respecting its significance in connection with prevention of the leaching action of rain water upon shoot tissues.

Reference has already been made to some recent work with fluorescence which suggests that sub-microscopic channels may exist in the epidermal walls by which salts may migrate to the outer surface of the cuticle. Such salts presumably must ultimately come from the protoplasts of the plant body, and their loss may be governed in the first place by factors controlling protoplasmic permeability. But one factor in preventing leaching must obviously be the extent to which the cuticle prevents wetting and penetration of the cellulose walls by rain.

Mann and Wallace have drawn attention to the possible practical importance of the leaching effects of rain in experiments upon the leaching of salts from the leaves of apple (24); whilst their experiments were carried out mainly by immersing leafy shoots for limited periods (24 hours and over) in distilled water, they showed reason for thinking that the same effects were operative in the field during rain. The losses of potassium salts in these experiments were very considerable, over 60% from detached leaves in 24 hours and over 15% from attached leaves in the variety Cox's Orange.

Wallace subsequently extended these observations to other fruit crops (53), but in spite of the practical significance of the observation the problem seemed to receive little attention until recently. It was emphasised that the loss must be from the living, undamaged leaf surface, but when immersion under distilled water is the method employed it is clear that changes in protoplasmic permeability, induced by the experimental conditions, may be a contributing factor. Ten years later the subject was reopened by Arens (5) who, on the basis of extensive experiments, argued not for a passive leaching of salts from the leaf by rain water, but for an active excretory process in the leaf as a fundamental component of its normal metabolic activity. As in Wallace's experiments, very marked losses of salts are recorded under the experimental conditions which usually, however, involved immersion of the leaf surface for periods of hours under distilled water. Observations were therefore directed by Lausberg (20) primarily to the problem of whether similar salt excretions were found under natural conditions as the result of the action of rain and dew. A loss of ash from 9% to 32% was

recorded from young leaves in natural rainfall; less was noticed from old leaves; and excretory loss was greater when the plants were grown in water culture if the original supply of salts in the culture was greater.

Lausberg and Arens are therefore thinking, not of a passive leaching process, but of a physiological mechanism regulating salt balance in the plant. Engel has recently failed completely to substantiate these results (10); some release of salts was always found from leaf surface wetted in water, but usually not more than 1% to 2% of the ash content was thus lost in 24 hours, and where larger losses were recorded it could usually be traced to loss of calcic carbonate. In view of the heavy losses, in potash salts particularly, reported from fruit by Wallace, this negative conclusion seems to be against the general run of evidence, although the case for any active excretory process in the plant obviously requires much further examination.

The whole question is of too great importance to be left in such a contradictory position, and indeed the whole question of the influence of the cuticle upon the functional activity of the plant requires much further exploration. Any such examination would necessarily include its effect upon growth. There are many observations in the literature which show that it cannot be neglected as a formative factor, controlling particularly surface extension as cuticular accumulation increases in thickness and solidity. There are also many observations which point to its significance in relation to penetration of various potential parasites when growing in contact with the shoot surface. It would extend this review too far to attempt to include these more specialised problems in the discussion.

SUMMARY

The cuticle is a layer of fat-soluble substances and of derivatives of such substances lying uninterruptedly over the outer epidermal wall of the herbaceous shoot in angiosperms. Whilst the inner layers of the wall have a cellulose base, no cellulose is present in the cuticle. The mode of formation of the cuticle is still debated; the case is once more restated for regarding it as the natural result, first, of accumulation of fatty substances at the outer air-water interface of the shoot, released mainly from epidermal protoplasts but also from deeper lying protoplasts; and second, of the subse-

quent chemical and physical changes undergone by such fatty substances which coalesce into an originally liquid film that oxidises and "dries" to a viscous and finally to a firm, solid film. This interpretation provides at the same time an exploration of the frequent presence of internal cuticular layers and of the general presence of fat-soluble and surface active substances in the walls of all tissues and of their release from such tissues under suitable conditions.

The outer epidermal wall is relatively complex in organisation; parallel to the surface it shows lamellation into cuticle, cutinised layers, layers rich in pectin and, to the inside, predominantly of cellulose. These lamellae may show a vertical discontinuity which conforms to the cell pattern of the epidermis, the cellulose basis of most layers showing interruption above the anticlinal epidermal walls. This complex organisation has been analysed for only a few special cases with thick outer epidermal walls, where its examination has been much facilitated by the polarising microscope, since the cutinised lamellae and the inner cellulose lamellae show contrasted anisotropic behaviour and are often separated by an isotropic, predominantly pectin layer. The anisotropy of the cutinised layers is due to the oriented solid wax deposited in the cellulose matrix. The vertical discontinuity of many of these lamellae and the extension of cutinised ribs or extensive pectin deposits over and into the anticlinal epidermal walls is explained by the fact that the last few divisions of the epidermal cells take place within parent cell walls which are already beginning to thicken and which are ruptured at a relatively early stage over the anticlinal walls.

Isolated flakes of cuticle often show a complicated relief pattern in surface view. This pattern develops from an originally smooth surface and may show changes during epidermal extension. A consistent explanation can be given of the influence of cell extension upon production of these varying patterns.

The cuticle seems the inevitable result of accumulation of unsaturated fatty substances on shoot surfaces; a different mode of apical growth explains its usual absence from the root surface. Its presence must influence almost all functional activities of the shoot, as, for example, transpiration, leaching effect of rain water and extension in surface of growing tissues.

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EFFECTS OF FIRE ON VEGETATION OF THE SOUTHEASTERN UNITED STATES¹

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INTRODUCTION AND HISTORICAL BACKGROUND

Among ecological factors affecting plant life of the southeastern United States fire holds a position of major importance. In many parts of this region present-day fires seem to exert an influence as great as that of climate and soil in determining the persistent type of vegetation. Of special significance is the fact that fires have been frequent in this region for many years. The ancient habit of woods-burning passed from Indians to the early white settlers to the extent that a law of North Carolina in 1731 required the burning of pastures and rangelands each March (22).

In this respect, of course, the Southeast is not alone. Fires became ecological factors throughout North America long before the first Europeans arrived (19, 69, 113). Fire is also ecologically

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important in other regions of the world, where, in some cases, the influence of burning has been exerted over many centuries (91, 150). Nevertheless, in the vegetation of the Southeast, effects of fire are more striking than elsewhere on this continent, and, with few exceptions, more striking than in any other region of the world.

In North America the ecological rôle of fire has been studied for 250 years. Historical highlights of particular interest to the Southeast have been observations (69) in 1691 on fire and the origin of prairies, references (14) in 1791 to fire and scrub barrens of the South, a study (123) of early stages in vegetational changes following fire in 1808, and early discussions in 1846, 1884 and 1888 of the southeastern longleaf forest as a fire-maintained type (96, 50, 95).

In spite of its importance, the ecological rôle of fire has been the subject of only two outstanding reviews. One (91), written from a world-wide viewpoint, omits the southeastern United States. The other (51) was not intended as a detailed account for any region. The present discussion is an attempt to answer the need for a general summary of the literature which contributes to a knowledge of the ecological rôle of fire in the southeastern United States.²

PLAN OF PROCEDURE

In order to obtain a satisfactory picture of the effects of fire on southeastern vegetation, certain points need to be considered for all frequencies of fire in the major plant communities of this region. These points are:

a) What part, if any, has fire had in the origin—bringing about the establishment—of the plant community or in maintaining and perpetuating it as a community?

b) What effect does fire have on the soil of the community?

c) What effect does the burning have on plants which survive,

d) How does fire affect the species-composition and floristics of the community?

e) For fire-maintained sub-climax communities, what successional changes take place if the community is freed from fire? (Hereafter this will be called "fire-relief succession".)

f) Is there a distinct "fire succession" for communities that are not fire sub-climaxes?

² More complete historical data and a general bibliography on fire effects can be found elsewhere (110, 150).

From the beginning it was apparent that, no matter how desirable, this plan could not be followed in its entirety. Fire effects studies have not been made for many communities, and if complete data were obtainable the number of plant communities in itself would prohibit the procedure. Furthermore, in most cases, there is a paucity of data on the comparative effects of different frequencies of fire. So that, in this review, plant communities are amalgamated into major vegetational types which, as far as possible, conform with types listed in discussions of the plant geography of the Southeast. With this amalgamation a fairly complete story can be obtained for most types.

In the interest of brevity and uniformity of thought, important considerations, such as fire and plant mutations (31) and decay resulting from fire wounding of trees (41, 71), are not included. In the interest of continuity references to specific investigators are few. A glance at the bibliography will give credit to those who have carried the burden of the research.

I. FORESTS OF THE LONGLEAF-SLASH PINE BELT

1. *Longleaf Pine Forest*

Rôle of fire in the origin of the longleaf pine forest. It is generally considered that in part of the Southeastern Coastal Plain, longleaf pine (*Pinus palustris* Mill.) and slash pine (*P. caribaea* Morelet.) grow in mixture. Recent observations, however, indicate that these pines usually tend to grow in almost pure stands and respond differently to fire (29, 37, 46, 76, 84, 86). Scattered patches of longleaf pine—pure, or mixed with other pines and scrub oaks—are also found on the dry eroded ridges of the upper Piedmont (34, 59). This longleaf forest is distinct in its ecological aspects, but its reaction to fire is much the same. The longleaf scrub-oak forest of the lowlands is treated as a separate type, since its responses to fire and other factors are quite different (120).

Whether the typical longleaf forest was originally established as a result of fire is purely a matter of conjecture; but since longleaf pine areas freed from the influence of fire change to other vegetational types (75, 76), it seems safe to agree with Eldredge (37) that "the great longleaf forest was ushered into the world" subject to frequent burning. Thus a preliminary hypothesis as to the origin of the longleaf forest might be advanced in this form: Fire

has brought about the establishment of longleaf forests on almost all areas of primary and secondary succession within the longleaf pine region, and has also brought about the same change in many areas originally occupied by other forest types.

Of course, any hypothesis referring to ecological changes which took place in the distant past is difficult to either prove or disprove unless there is opportunity to observe a similar change now taking place. Unfortunately, in the present case, there is almost no possibility of observing such a change, since the longleaf forest appears to have already reached its maximum extent and is now undergoing considerable reduction (86).

Rôle of fire in perpetuation of the longleaf pine forest. Much valid evidence indicates that fire is the main factor responsible for perpetuation and maintenance of longleaf pine in its typical forest stands (26, 37). In the first place there is a greatly increased percentage of germination of longleaf pine seed on areas burned over shortly before seed fall (25, 26, 27, 28, 36, 138). About twice as many seeds germinate on freshly burned plots as on protected areas (115, 153, 183). Chapman (26) indicates that this increased germination is a response to exposure of the mineral soil, since the scanty reproduction which does take place in protected forests is almost always confined to bare areas. Obviously, fire is the only agent which can expose any considerable areas of mineral soil in a forest. Greenhouse studies have shown that leaf ashes have a slightly stimulating effect on germination of longleaf seeds (42), but the mechanical effect of the mineral soil is undoubtedly much more important.

If fire perpetuates the longleaf forest, it must also promote establishment and survival of these numerous longleaf seedlings. In this respect, however, the evidence seems paradoxical at first glance. Gemmer and others (42) have shown that the layer of ashes which stimulates seed germination may decrease seedling survival through inhibiting radicle penetration. Exclusion of fire after establishment has been shown to increase seedling survival as much as 67% in some cases and up to 800% in others (153, 156). However, these more numerous seedlings on areas unburned after seed germination show little or no growth, are "sickly" in appearance and are probably doomed (26, 153). These seedlings on areas completely protected from fire after seed germination usually remain

in the stunted "grass" stage until they are destroyed by hogs (52), catastrophic fires (156) or competition of the surrounding grasses. The fewer seedlings surviving on periodically winter-burned areas become permanently established and initiate height growth. Several years ago Andrews (6) pointed out the great difference in establishment of longleaf seedlings on burned as opposed to unburned areas.

One important way in which fire promotes permanent establishment of longleaf pine is in the removal of vegetation which surrounds the slow-growing longleaf seedlings (25, 27, 36, 46, 121, 160). Another is by partial control of the brown-spot needle disease (133, 134). The remarkable resistance of longleaf seedlings to fires which kill other vegetation is due, in the main, to three factors (26): *a*) almost all growth of longleaf for the first five years is concentrated in the roots, giving an adequate supply of food for growth of new leaves when fire consumes the foliage; *b*) the buds are well protected by a tuft of leaves; *c*) the bark is abnormally thick.

There are, of course, conditions under which fire destroys longleaf pine seedlings. They are quite susceptible to burning during the first year after germination (76, 86), and annual burning, begun more than a year after germination, has the same stunting effect as complete absence of fire (156). Longleaf seedlings undergo rapid height elongation in their sixth to eighth year, and during this period they are readily killed by fire (23, 26, 133, 134, 153, 167). Fires after several fire-free years destroy many young longleaf pines, since an intense heat is created by the burning of the accumulated grass and litter. The season during which fire occurs also influences the final result. Fall fires frequently kill all longleaf pines under ten feet in height, while spring fires may kill up to 50% of the young trees (25). In some cases severe fires during the dry windy season become crown fires and kill many mature trees, and frequently destroy 100% of the longleaf poles (156).

It is, therefore, not so much fire which these researches indicate as essential to perpetuation of the pure longleaf forest as it is a proper ratio of winter fires to fire-free years. Fires must occur often enough to bring about those conditions necessary for germination, growth and establishment of longleaf, and prevent accumulation of litter. If such burning is to result in the effects accredited

to it, there must be non-fire years so spaced that many of the established seedlings can pass through the critical first and sixth to eighth years without being exposed to fire.

The idea that fire is an essential factor in the longleaf forest dates back at least to 1846 (96). Harper (59, 61, 67) has been largely responsible for keeping the idea alive, and others (25, 28, 76, 153) have been outstanding in presenting supporting data. This radical theory, however, has always met with much opposition. In 1897 (108), 1908 (81), 1913 (83) and 1937 (114) reputable scientists maintained that fire is destructive, not essential, in the longleaf forest. Most recently, Terry (148) concludes that effects of fire on the longleaf forest are all detrimental and that soil and other environmental factors are responsible for the pure longleaf forests.

Without entering into controversy over controlled burning in the longleaf region (29), one must admit that the evidence indicates that, within the very narrow and definite limits outlined, fire promotes and probably is essential to perpetuation of longleaf forests. Statistical evidence opposing this theory is almost entirely lacking, so that the burden of proof is on those who oppose.

Effects of fire on soil of longleaf pine forest. The effects immediately apparent following burning of vegetation are death of many plants and changes in the physical and chemical nature of the soil. The former is a phase of the change in species-composition. For the present, however, the latter will have to be treated as a distinct effect, since few efforts have been made to correlate such soil changes with vegetational changes.

Heyward's study of 44 fires in the longleaf region (74) show that during fires temperatures within the upper quarter inch of soil usually reach 150° to 175° F. for a period of two to four minutes, then drop abruptly. At one-half inch, temperatures range from no change to a rise to 190° in extreme cases. At one inch, only a slight increase can be measured. None of these temperatures approaches the charring point for organic matter, but it is apparent that perennial plants having most roots in the upper inch of soil are more likely to be eliminated by fire than more deeply rooted species. Almost all ungerminated seeds are destroyed during fires.

Counts have shown only one-fifth as many animals in a unit volume of frequently burned longleaf soil as in unburned soils, and the unburned soils have as much as 11 times as many animals in the

upper two inches (73, 79). On the other hand, higher bacterial counts are reported for the burned areas (48, 156), but the figures given—385,000 more bacteria per acre—show that little importance can be attached to this increase.

Burned-over longleaf soils are somewhat exposed by the partial destruction of the ground cover. Several changes in the physical nature of the soil result from this exposure. Soil temperatures may average as much as 5.5° F. higher for burned areas (156), possibly largely due to the heat-absorbing capacity of charcoal. Soil moisture is as much as 50% lower in burned soils (72, 156), and with repeated burning the water-absorbing ability of longleaf soils is decreased from 50% to 80% (153, 156). Decrease in water-retaining ability is neither large nor consistent.

Continued burning brings about a grassland type of humus and an absence of an A_0 horizon in the longleaf forest (73, 78, 79). The A_1 structure varies from single grain to massive, while fine structure holds throughout the unburned soil (73). Mechanical penetrability tests show unburned soils to be one to five times softer than the same soil when burned frequently (72, 155, 156).

Results of studies of effects of fire on the chemical nature of longleaf pine soil are somewhat contradictory. Some early observers felt that burning impoverishes longleaf soil (128), and others stated that the minerals returned to the soil by burning are of great benefit (57). Results of quantitative studies of the chemical nature of longleaf forest soil before and after burning also differ widely (12, 77). Barnette and Hester (12) studied a soil burned annually for 42 years and compared it with a similar soil completely protected from fire. They estimated that 2,088 pounds of organic matter and 27 pounds of nitrogen are lost per acre per year through burning. They found exchangeable lime higher in the upper inch of burned soil, and lower below one inch, than in the unburned soil. Wahlenberg (155) found organic matter and nitrogen slightly lower in burned-over soils.

Other studies comparing longleaf soils, burned-over frequently, with protected soils have given results of an opposite nature. They (72, 77, 156) show that longleaf soil of frequently burned areas is slightly less acid and has up to 100% more replaceable calcium. Combustion tests show these burned soils to have greater organic

matter content (47, 48, 72, 77, 156), possibly due to charcoal deposition (72, 77). Higher total nitrogen is also reported for these burned soils (47, 48, 72, 156). Since more grass and legumes are found on burned-over longleaf areas, one possible source of this additional nitrogen is obvious (47, 62, 156). The main soil changes as a result of fire, however, seem to be due to the return of mineral materials to the soil in the ashes. Even though heat increases the soluble material in soils (130, 131), the temperatures during fire are high enough to bring about chemical changes only in the upper half inch of the mineral soil (74).

These opposing results are hard to reconcile, but a partial explanation may be found in the differences between effects of fire on soil of a longleaf forest on abandoned fields, and effects on soil of a virgin forest (77). The virgin area showed the increases mentioned above for burned-over soil. The frequently burned abandoned field soil was lower in nitrogen and organic matter than the unburned old-field area. This difference is probably due to the scarcity of herbaceous vegetation on the abandoned cultivated area. Within limits, therefore, it seems safe to conclude that burning, by returning minerals to the soil and by promoting growth of ground-cover plants, usually increases organic matter, nitrogen and replaceable calcium in most longleaf forest soils. Such changes are conditioned by the past history of the soil, and may even be in the opposite direction.

Effects of fire on plants surviving the burning of longleaf forests. When fires sweep through longleaf pine forests the effects upon surviving trees are determined by such factors as age of the trees, and frequency and season of burning.

For longleaf seedlings summer fires may immediately be eliminated from consideration, since such fires usually leave few or no seedlings. Frequent winter fires may cause as much as 50% retardation in height growth of longleaf seedlings (167). The amount of retardation varies with the severity of defoliation (32). Longleaf seedlings subjected to annual winter burning are kept in the "grass" stage—or stage in which no height growth takes place—almost indefinitely (153, 156). However, seedlings of the same age on unburned areas likewise initiate no height growth (156).

Seedlings on areas winter-burned at intervals of about three years may show twice as much growth as those not exposed to fire (134).

This increase in growth is attributed, in part, to control of the brown-spot disease caused by *Septoria acicola* (Thum.) Sacc. Fire consumes the inoculum in the fallen leaves and in the dryer older leaves, thereby reducing the possibility of infection of the new leaves. A single winter fire may almost eliminate the disease for one season, but by the end of the second fire-free season, seedlings on burned areas usually appear as infected as those on unburned areas, though some may show as much as 50% fewer spots (133, 134). The third season without fire usually sees the brown-spot disease again in full development. Without presenting data, Wheeler (29) has questioned the decrease in brown-spot as a result of fire, but the actual data presented (26, 133, 134) will have to be accepted unless contradicted by other checks.

Other factors, such as removal of competing vegetation (120) and return of minerals to the soil by burning (58, 96), also undoubtedly are effective in any instance in which elongation of longleaf seedlings is promoted by infrequent burning.

Longleaf saplings show retarded growth as a result of frequent burning in either winter or summer. Measurements reveal from 20% to 50% decrease in height growth, and from 25% to 66% decrease in diameter growth for saplings on areas burned frequently or annually (99, 100, 101, 155, 156). A reduction in the annual basal area increase of 22% to 44% is reported for annually burned young longleaf pine forests (100, 101, 104). In these frequently burned trees sometimes no annual ring or only a trace of spring wood is formed in the growing season following a severe fire (32, 43). Thereafter recovery to normal growth is rapid. Bark on annually or frequently burned trees may be as much as .2 inch thinner than on unburned trees, but, obviously, this is unimportant (102, 154).

Burning, annually or otherwise, has little effect on either growth of mature longleaf pines or on cone and seed production (153, 156), but frequent burning may result in basal wounding of as many as 25% of the mature longleaf pines (35). This indicates that longleaf is more susceptible to this type of injury than are other important southern pines, for shortleaf pine shows basal injury on as low as 11% (35), and, in other areas, loblolly pine burned almost every year may have only 16% fire-scarred trees (41). Gum yield in both mature and sapling longleafs may be reduced as much as 50%

the first year after a fire (11, 23, 118, 139). Recovery is rapid, so that peak yields may again be reached within nine months (139) or, in extreme cases, within two years (118). But trees scorched so severely as to be devoid of needles usually show no external evidence of injury six weeks later (76), so that for trees surviving the burning, injury is almost entirely internal.

It has been suggested that fire may have some physiological effect which initiates early expression of dominance in some longleaf seedlings (153). This remains to be investigated.

Effect of fire on species-composition of the longleaf forest. Evidence presented above indicates that frequent but not annual winter fires are largely responsible for germination, permanent establishment and early growth of longleaf pine. Thus burning favors longleaf pine, removes competition and brings about the familiar type of longleaf forest in which other trees and underbrush and herbs are very scarce (76).

Fire destroys seedlings of other pines growing with longleaf (26, 46, 160). Chapman (26) has pointed out that other southern pines survive fires at frequencies of 10 to 15 years but cannot survive fires of the three to four-year frequency usually found in the longleaf forest. The inability of other southern pines to survive fires during the first years of their existence is due to a rapid initial stem growth which does not occur in longleaf pine (46). Comparative counts made after three years of annual burning of a forest nursery plantation showed survival of longleaf to be 40 times as great as that of loblolly, 14 times that of slash pine, and seven times that of shortleaf, including shortleaf sprouts (160). Even black jack oak (*Quercus marilandica* Muench) sprout competition is removed by frequent fires (25).

Fire and fire-relief succession in the longleaf pine forest. As indicated, the longleaf pine forest is universally considered to be a fire sub-climax. There are a very few instances, however, in which areas are changed from longleaf pine to other types by frequent fire combined with other factors. Logging of longleaf pine on very moist sandy areas, if followed by fire, may bring in a *Campulosus-Panicum* type of bog which remains a treeless "savannah" in spite of the presence of longleaf seed trees (120, 165). Apparently, this is due to a change in the physical condition of the soil resulting from fire and exposure (120). Longleaf seedlings can not overcome

competition of the invading moist site herbs and are destroyed by the repeated burning. Another case in which fire may aid in converting a longleaf forest to another forest type is discussed in connection with the longleaf-scrub oak type.

Since longleaf is a fire sub-climax type, the successions of particular interest are those which take place in longleaf forests following exclusion of fire. The major fire-relief successions observed or suggested by reliable evidence are indicated in the following diagrams: Successions 1 to 5 are from Heyward (76), 6 to 8 from Pessin (120). As indicated, locality, soil and drainage are of importance in determining the type of fire-relief succession.

Type of longleaf forest	Next stage(s) in succession. (With years, if noted.)
1. Lowland, abandoned fields	Wax myrtle (<i>Myrica cerifera</i> L.) Laurel oak (<i>Quercus laurifolia</i> Michx.) (12-15 years)
2. Rough, poorly drained lowlands	Water oak (<i>Q. nigra</i> L.) Red gum (<i>Liquidambar styraciflua</i> L.)
3. Virgin forest, lowlands	Laurel oak, live oak (<i>Q. virginiana</i> Mill. and varieties) with undergrowth of wax myrtle, red bay (<i>Persea borbonia</i> (L.) Pax) and holly (<i>Ilex</i> spp.) (75 years).
4. Areas near lakes, in lowlands	Slash pine → Laurel oak, water oak, red gum
5. Well drained areas in upper coastal plain	Southern red oak (<i>Q. rubra</i> L.), Post oak (<i>Q. stellata</i> Wang.) Loblolly pine (<i>Pinus taeda</i> L.) Shortleaf pine (<i>P. echinata</i> Mill.)
6. Dry, loamy flatwoods	Southern red oak → oak-hickory Red gum, post oak
7. Moist, sandy flatwoods	beech-maple Cypress (<i>Taxodium</i> spp.)-Tupelo (<i>Nyssa</i> spp.)-swamps
8. Loamy flatwoods, moister slopes	Black gum (<i>Nyssa sylvatica</i> Marsh) Loblolly pine, sweet gum in thickets
	Oak-hickory

Effects of fire on the herb- and shrub-composition of the longleaf forest. Throughout the Southeast much of the longleaf forest is used for cattle range. Whether the more open areas were selected for range, or use for range has made them more open, is not clear from existing literature. Perhaps there is little difference in tree density between the range and non-range areas, but sparsity of shrubs and the presence of "scrub" herbs in the typical longleaf forest has long been recognized and blamed on fire (40). This

indicates some difference in ground cover between areas used for grazing and those not so used.

The effect of fire on the grasses, other herbs and shrubs is of interest to ecologists, cattle growers, game preserve managers and bee-keepers. Results obtained by numerous investigators—mainly Greene, Wahlenberg and Stoddard—are in almost complete agreement as to these effects. Since summer fires result in destruction of most of the ground cover, the following summary refers mainly to annual or frequent winter fires.

Considerable reduction in the area and quantity of grasses and other herbs results from complete fire protection in longleaf forest grazing areas. In six years grazing areas decreased twice as rapidly on fire-protected range as on adjacent winter-burned range (156). Over twice as many green-weight pounds of grass can be found per acre on burned areas as can be found on comparable unburned areas (47). This difference is probably due partially to deposited ashes (80), and partially to the removal of pine reproduction (156). The herbage also begins growth earlier on burned longleaf areas (21, 47). This is undoubtedly due to the higher soil temperatures reported for burned-over ranges (47).

Fire also influences the species-composition of the ground covering. Wiregrass (*Muhlenbergia expansa* (DC.) Trin.) and broomsedge (*Andropogon virginicus* L.) are almost entirely eliminated by burning, while the introduced carpet grass (*Axonopus compressus* (Swartz) Beauv.) is unaffected (77, 147, 155, 156). Two of the principal native grasses of the longleaf region, the big and little bluestems (*Andropogon scoparius* Michx. and *A. tener* (Nees) Kunth.), are thinned out by accumulation of litter resulting from fire protection; but they remain vigorous on burned areas (155). The reaction of these andropogons to fire vary with intensity of grazing (156). On ungrazed-unburned areas *A. tener* decreases, but on burned-grazed areas *A. tener* increases and *A. scoparius* decreases. On grazed areas *A. tener* increases with burning, while *A. scoparius* decreases. Even though these grasses are maintained in greater abundance on grazed-burned areas than on unburned areas, this ten-year study showed a gradual decrease in the percentage of the total herbage which was made up of these two grasses, and the percentage of weeds gradually increased. On ungrazed areas there was no change in the weed population with

burning, but on areas severely burned because of litter accumulation, the grasses are almost completely replaced by a weed community composed mainly of *Solidago odora* Ait. The ability of some grasses to either increase or remain prominent when subjected to fire is largely due to deep root systems which enable them to survive, while competing plants are killed by the fire (21).

Wheeler (29) believes that some of these andropogon areas had been subjected to overgrazing and that burning kept this overgrazing from continuing, thereby permitting reproduction to increase. He gives no data to support this contention.

Grasses growing on areas subjected to burning for ten years show slightly higher percentages of protein, lime, phosphate, ash and fat than the same species growing on unburned areas. Grass from unburned areas has a greater bulk and crude fiber content, but the green dry weight is much lower (155, 156). These differences are undoubtedly due to the accumulation of mineral matter as ashes in the burned soil so that there is a possibility that these differences might not hold over a greater period of years.

Other herbs also respond to burning-over of the longleaf forest floor (62). A tally revealed 11 species of legumes on unburned and grazed areas in Mississippi, while adjacent burned-grazed areas showed 16 species of legumes (156). Numbers given for this same Mississippi area are 23,900 more legume plants per acre on burned-ungrazed plots and 8,100 more per acre on burned-grazed plots (85). Genera of legumes, such as *Chamaecrista*, *Lespedeza*, *Dolicholus* and *Meibomia*, become numerous on former broomsedge and wiregrass areas following fire (48, 77, 145, 146, 147, 156). Annual lespedeza (*Lespedeza striata* (Thumb.) H. & A.) invades burned areas rapidly when a source of seed is available, as also does the composite genus *Chrysopsis* (77, 147). Perennial legumes are prominent following fire because of their ability to sprout, and because fire acts as a seed-scarifying agent (93).

In general, shrubs are scarce in the burned longleaf forest (40). Natives sometimes use fire in an attempt to promote growth of huckleberries (*Gaylussacia* spp.), but continued burning sometimes results in elimination of such shrubs (149). Stoddard (147) found that an occasional fire has a stimulating pruning effect on huckleberries, blackberries and dewberries (*Rubus* spp.). There are no fruits during the season immediately after a fire, but increased bearing is evident the next few years.

2. Longleaf-Scrub Oak Forest

Rôle of fire in the origin of the longleaf-scrub oak forest. This distinct type of forest is found in scattered patches in the typical longleaf forest. The longleaf pine is predominant, and, in direct contrast to the absence of understory in the longleaf forest, there is a prominent understory of small sprouting scrub oaks, such as turkey oak (*Quercus catesbaei* Michx.), scrub post oak (*Q. stellata* var. *margaretta* (Ashe) Sarg.), scrub live-oak (*Q. virginiana* var. *geminata* Sarg.), bluejack oak (*Q. cinera* Michx.), southern red oak and blackjack oak. In 1791 it was proposed that this scrub oak-pine type originates from the typical longleaf type as a result of very frequent fires (14), but, to the present, the more available ecological literature contains nothing which can be said to offer any data bearing directly on the origin of this forest.

Statements by Howell (84) indicate indirectly that such forests may originate from logging practices which leave an abundance of scrub-oak seed trees and few or no longleaf seed trees. It is also possible to interpret certain of Chapman's statements (26) as indicating a belief that a longleaf-scrub oak forest may result from frequent fires following logging of a slash pine area. Pessin (120) seems to hold a similar conception, but Heyward (76) stresses the importance of soil in this vegetational type and apparently feels that fire has little to do with its establishment.

The salient points of this indirect evidence may be combined into a theory of the origin of this forest: Within small natural or artificial openings in a typical longleaf forest—or more rarely in a slash pine forest—when seed trees are available, scrub oak reproduction will appear on soil which is so dry and sandy that other plants grow poorly and are unable to compete with the oaks. Annual or frequent burning thereafter increases the scrub oaks through sprouting, and longleaf production is destroyed in the competition. From these nests of scrub oak thickets, with continued frequent burning, these oaks will spread through the forest beneath the mature pines.

Effect of fire on plants surviving and on species-composition of the longleaf-scrub oak forest. The effect of fire on the longleaf pines in this forest will be much the same as in the longleaf forest. The scrub oaks are seldom killed by fire, but show a remarkable ability to continue sprouting when the tops are repeatedly killed

back (120). It is to be expected that stunted growth results from this repeated burning (118). If these oaks become larger than eight inches d.b.h., their ability to sprout is considerably lessened (76).

The longleaf-scrub oak forest is the outstanding exception to the rule that unprotected forests containing longleaf pines are different from those furnished fire protection (76). In North Carolina, however, on lower more moist soils a transition zone is formed between the longleaf-scrub oak forest and bog pocosin vegetation. With continued burning the oaks in this transition are eliminated and semi-bog grasses, sedges and other herbs take their place (162). This seems to be the only instance in which the composition of longleaf-scrub oak forests is changed by fire.

Fire and fire-relief succession in the longleaf-scrub oak forest. Interaction of fire, logging and soil sometimes brings about successional changes in this vegetational type. As in the longleaf forest, many of these changes follow protection of areas once frequently burned. These changes are represented in the following:

Report	Conditions	Next stage(s) in succession
(162)	Frequent burning on low, moist slopes	Grass-sedge semi-bog
(84)	Frequent burning following removal of all seed trees	Pure scrub oak type
(120)	No fires, or infrequent fires	Pure longleaf pine → oak-hickory
(76)	Heavy or complete cutting of pine, then infrequent fires on dry sandy ridges	Oak-hickory (direct) Pure scrub oak → oak-hickory
(120)	Frequent fires, or no fires, no cutting; or very light cutting, on well drained, sandy soil	No change, remains longleaf-scrub oak

3. Slash Pine Forest

Rôle of fire in the origin of the slash pine forest. There are two theories as to the origin of the slash pine forest in the southern part of the longleaf-slash pine belt. Both theories involve fire.

Harper (54) thinks the slash pine, coontie (*Zamia* spp.), saw palmetto (*Serenoa repens* (Bartr.) Small) of Florida originated when these species invaded areas where evergreen hardwoods—now found only in hammocks—had been eliminated by fire. Small (136), who believed that fires are recent factors in this region, elaborated on the action of fire in slacking the underlying limestone

which initiates erosion and speeds elimination of hardwoods. Small believed that slash pine was established in Florida when seeds blew into this burned-eroded area from the Caribbean islands. Pure stands of slash pine sometimes result from dry-season fires in the southern white cedar swamp type (88, 90) (see discussion of the latter type for details). Recently, a "fire sub-climax of slash pine, *Quercus geminata* Small, and *Q. myrtifolia* Willd." has been described for an island in the Mississippi (117).

Harshburger (68) maintained that were fire responsible for introduction and establishment of slash pine forests there would be no other type of forest in this frequently burned region. Ineson and Eldredge (86) have indicated that in frequently burned regions of the longleaf-slash pine belt, slash pine is confined to those moist situations which escape repeated burning; so that, as a result of fire protection, the slash pine, which grows faster in early stages than longleaf, has invaded and taken over extensive areas of the longleaf forest. Other observers hold similar views (37, 76, 84, 122).

Both these theories are based on scientific observations. By combining them it would appear that slash pine is more fire-tolerant than most hardwoods and less fire-tolerant than longleaf pine. Thus slash pine can invade and maintain control over former hardwood areas, as in southern Florida, following repeated burning, but it can invade longleaf areas only when the fire-frequency which favors longleaf is lessened.

Effect of fire on plants surviving and on species-composition of the slash pine forest. Fires occurring after establishment of slash pine forests may have important effects on the composition of this forest. An increase in slash pine seedlings has been observed the summer after a winter fire, but this increase is not so marked as with longleaf pine (115). Greenhouse tests have shown germination of slash pine to be only slightly stimulated by leaf ashes, and slash pine humus has an equally stimulating effect (45). Apparently, therefore, germination of slash pine seed is little affected by fire.

Radicle penetration and survival of slash pine seedlings is higher when there are no ashes over the soil, and under such conditions slash pine seedlings may show as much as 50% higher radicle penetration than longleaf seedlings (45). This may be one factor

promoting invasion of protected longleaf areas by slash pine. A light burning may kill all slash pine seedlings under four years old (114), and survival of slash pine seedlings after fire may be only 60% that of shortleaf, and only 10% that of longleaf in the same area (160). Frequent fires in a slash pine forest will eliminate the slash pine, since its germination, survival and permanent establishment are hindered by fire. Chapman (26) estimates that intervals of ten fire-free years are necessary for perpetuation of slash pine.

Once slash pine has passed through the seedling stage, however, it seems to be almost as fire-tolerant as longleaf pine (24, 76). A single winter fire may cause as much as 25% reduction in growth the next season (150), but in thinned stands of slash pine burning usually has little effect on height growth (140).

Among other plants of the slash pine forest, definite fire-effects information is available only on coontie and saw palmetto, as found in Florida. By prolific sprouting from large underground stems these plants are increased by fires (136). Small (136) maintained that the pine forest coontie (*Zamia integrifolia* Ait.) is a new species which arose from the coontie now found only in hammocks (*Z. silvicola* Small.) as a result of continued burning. Undoubtedly the effects of fire on soil, grasses and herbs of the slash pine forest will be much the same as in the longleaf forest.

Fire and fire-relief succession in the slash pine forest.

Report	Conditions	Next stage(s) in succession
(116)	Slash pine, scrub live oak, scrub oak, with fire protection	<i>Quercus virginiana</i> Mill. <i>Sabal glabra</i> Sarg.
(120)	Slash pine, saw palmetto, <i>Ilex glabra</i> (L.) A. Gray on moist sandy flatwoods. Cutting of all pines, then frequent fires	<i>Campulosus</i> } <i>Xyris</i> } in bogs <i>Rhexia</i> } <i>Sarracenia</i> }
(76)	Slash pine, with fire protection	<i>Quercus laurifolia</i> Michx. <i>Q. nigra</i> L. <i>Nyssa</i> spp.
(35A)	Slash pine, coontie, saw palmetto. No fire	Hammock evergreens. (See "hammocks".)
(26)	Slash pine. Cutting of pine, then fire more often than ten-year intervals	Sprouting scrub-hardwoods

4. "Scrub" Forest

Rôle of fire in the origin and perpetuation of scrub forest. Another distinct type of forest, known as scrub, is scattered through the longleaf-slash pine belt in the South. This forest is made up

of sand pine (*Pinus clausa* (Engelm.) Sarg.) and the various scrub oaks mentioned as components of the longleaf-scrub oak forest. Scrub wild oak (*Quercus myrtifolia* Willd.) and Chapman's scrub oak (*Q. chapmanii* Sarg.) are also prominent in this scrub forest, and various evergreen shrubs furnish an understory.

Some evidence indicates that this scrub forest became differentiated from the surrounding "high-pine" forest on areas of soil too poor to support other vegetation and that absence of fire maintains it as a distinct type (159). The nature of this forest gives it somewhat of a natural resistance to fire. Most of the oaks and shrubs are evergreen, and the absence of ground cover in the surrounding pine forest gives an isolating fire break.

It is also possible that sand pine-scrub oaks forests of coastal dunes are sometimes established and maintained through the influence of fire in promoting sprouting of the oaks (120).

Most of the evidence indicates that other factors than fire, such as differences in soil and water relations, account for the difference between the high pine and scrub forest (109). Fires usually sweep this forest but once in the life-time of the pines (67). Albert states (2) that there is little information on the establishment of the large sand pine areas, but that it is doubtful that invasion of this type of forest following fire is ever important.

Effects of fire on species-composition of the scrub forest. Accounts of changes in composition of this forest following burning are somewhat confusing. Sand pine trees hold their cones unopened for several years, and these cones open only after the tree is cut or killed by fire (2, 53). It has been reported, therefore, that sand pine seedlings appear in large numbers and take over scrub areas following fire (53, 61, 62, 63). It has also been reported that burning increases the sprouting oaks so much that pines rarely take over scrub areas after fire (159).

As indicated by Albert³ (2), both these observations are correct. Due to evergreen constituents the scrub usually burns only in the spring when high winds make for crown fires which kill most of the pines. The end result following fire depends upon age of the pine at time of burning. When cone-bearing pines are killed, the sand pine is favored in the regeneration. When two fires occur

³ Mr. Albert cautions that his statements—transmitted by letter—are based on several years' observation, and not on "specific studies". Mr. Albert's experience makes his observations worth much consideration.

closely enough together that the pines are not old enough to bear cones, the pine will be eliminated.

Fire and fire relief succession in the scrub forest.

Report	Conditions	Next stage(s) in succession
(120)	Forest on dunes, no fire	Longleaf pine → oak-hickory
(120)	Forest on dunes, infrequent fires	Longleaf pine
(62)	Fires once in lifetime of pines	No change, scrub remains
(63)	on dunes	
(159)	Fire destroying scrub forest	Turkey oak, bluejack oak scrub
(2)	Fire in young, non-cone-bearing pines	Scrub oak, scrub myrtle barrens
(2)	Crown fires in older sand pine	No change, sand pine regenerated

II. COASTAL PLAIN AND BOTTOMLAND HARDWOOD FORESTS

5. *Bottomland and Mississippi Delta Hardwood Forests*

Little information is available concerning the rôle of fire in the lowland hardwoods of the Coastal Plain. Such hardwoods as laurel oak (*Quercus laurifolia* Michx.), water oak (*Q. nigra* L.), red gum (*Liquidambar styraciflua* L.), black gum (*Nyssa sylvatica* Marsh) and red maple, usually associated with slash pine in protected areas around ponds, frequently spread into the longleaf forest as a result of fire protection (76). Thus the slash pine forest which takes over longleaf areas under fire protection may itself be replaced by a lowland hardwood forest if fire prevention is continued.

In some areas of the Mississippi Delta forest reproduction is lacking due to fire (166). Possibly continued burning of this forest may eliminate it. In a study of decay following fire in this region Hepting (71) observed that few saplings break over and disappear from the stand as a result of fire injury.

6. *Coastal Plain Scrub Oak Forests*

Rôle of fire in origin of scrub oak forest. All accounts of the origin of the turkey and bluejack oak forests of the Southeastern Coastal Plain involve fire. In Mississippi longleaf forests change to scrub oak as a result of clear cutting followed by annual burning (84). In Florida lumbering permits growth of herbs up to the edge of the sand pine-scrub oak forest so that fire gets into the scrub and soon turkey and bluejack oak replace the evergreen oaks and pine (159). In the longleaf-scrub oak forest continued burning after establishment of the oaks kills longleaf seedlings before they

get out of the grass stage, and the forest becomes a pure stand of scrub oaks (120). Studies in the coarse sand region of North Carolina show that a combination of coarse sand, dry vegetation and fire usually maintains distinct types of vegetation within this area (162, 165). In one of these types wire grass (*Aristida stricta* Michx.) is dominant with turkey oak as sub-dominant. This is a pioneer stage in succession following lumbering, cultivation or other disturbances and is found on dry sandy areas with low water tables if fires are frequent.

Effect of fire on plants, species-composition and succession in the scrub oak forest. Since scrub oaks sprout prolifically, the number of oak stems per acre is greatly increased after fire (120, 165). Though seldom killed by fire, the suppressed condition of these oaks is due to repeated burning (120). In the North Carolina sand-hills turkey oak does not become dominant over wire grass unless protected (162, 165). Certain characteristic pioneer plants, such as cladonias (*Cladonia* spp.), sand selaginella (*Selaginella acantho-nata* L.), wire plant (*Stipulicida setacea* Michx.) and *Polygonella polygama* (Vent.) A. Gray, also become characteristic of the wire grass-oak community following fire. The low water content of these fire-promoted plants predisposes them to fire, and thus a vicious cycle is set up (165).

Since this forest is a result of fire and is a fire-sub-climax, the only further successions will be fire-relief successions, as follows:

Report	Conditions	Next stage(s) in succession
(165)	Frequent fires	No change, scrub maintained
(120)	Infrequent fires	Longleaf sub-climax
(165)	No fire in wire grass-oak	Blackjack oak
		↓
		on dry areas oak-hickory
		↘ on moister areas beech-maple
(120)	Complete fire protection in Mississippi scrub	On dry areas longleaf sub-climax
		↓
		On moist areas oak-hickory

7. Southeastern Hammocks

The vegetation of the Florida and Alabama hammocks is made up of evergreen shrubs, small evergreen trees, such as evergreen oaks and the loblolly magnolia (*Magnolia grandiflora* L.), various hickories and other hardwoods. In the southern Florida hammocks

are found such additional species as lancewood (*Nectandria coriacea* Sw.) and cherry laurel (*Laurocerasus myrtifolia* (L.) Britt.). The shrubs vary with locality and include coontie, wax myrtle and gall berry (*Ilex glabra* L.) A. Gray (60, 124).

There is no agreement as to the rôle of fire in the origin of these hammocks. Some hold that this type has become differentiated in response to soil differences (68). Others state that hammocks can not be correlated with altitude or subsoil (136). In some cases it is thought that certain areas within the fire-swept pine forest have somehow escaped fire so that humus accumulated and the additional moisture allowed the evergreen-hardwood type to become established (54, 66, 124, 125). A middle view is that hammocks originated on any area—protected or otherwise—where oaks invaded the pinelands and furnished shade and humus for other tolerant species (17, 125). Apparently, hammocks are both the next stage from pines in normal succession and also the climax forest for the region in question (54, 66, 124, 125). Whether all hammocks originated on areas escaping fire is unimportant. They are quite easily destroyed by fire (124, 125).

Since hammocks are a climax type, there can be no further succession except following fire. Only one instance of such fire-succession has been recorded. Apparently, fire sometimes destroys hammock vegetation and changes the drainage so that the area becomes a *Campulosus-Xyris* bog (120).

8. *Pocosins*

The pocosins of eastern North Carolina in which the vegetation is mainly evergreen shrubs, such as wax myrtle and gall berry with a few pond pines (*Pinus serotina* Michx.), are closely related to the hammocks. Wells (163) holds that many of these pocosin bogs are due to a combination of poor drainage, fluctuating water table and infrequent fires. Others appear to have originated on partly protected semi-swamp areas from which longleaf pine has been removed (161).

Unlike hammocks the pocosins can regenerate after fire if the fire occurs during wet seasons (161, 163). Fires during dry seasons result in various successional changes as follows (162, 163, 164):

Condition	Next stage(s) in succession
Mineral soil, frequent fire	Grass-sedge bog
Peat soil, fire in dry season	Fire-moss (<i>Funaria</i> sp.)
	Golden rod (<i>Solidago fistulosa</i> Mill.)
Infrequent fires or complete burning on certain areas	<i>Arundinaria-Ilex</i> → Next stage see "savannahs"
No fire	<i>Ilex-Myrica</i> dry bog → Oak-hickory →
	Beech-maple
<i>Ilex-Myrica</i> pocosin frequent fire	<i>Aristida-Vaccinium</i> fire sub-climax

III. COASTAL PLAIN SWAMP FORESTS

9. Cypress Swamps

Cypress swamps (*Taxodium* spp.) of the Southeast are frequently swept by fire during dry seasons. In some cases these fires seem to have little effect (61), but in other instances frequent fire may change a cypress swamp to a shrub-choked open area in which gall berry (*Cyrilla racemiflora* L.), and other shrubs predominate (162). On the other hand, cypress-tupelo swamps sometimes originate from fire-protected longleaf areas (120).

10. Southern White Cedar Swamps

Extensive areas along the southeastern coast are occupied by southern white cedar (*Chamaecyparis thyoides* (L.) B.S.P.) swamps. Associated species vary from black gum, red maple and pond pine in North Carolina to slash pine, cypress and sweet bay (*Magnolia virginiana* L.) farther south.

A fire in this swamp forest usually destroys almost all the white cedar trees regardless of age (88, 90). If the swamp burns during the wet season and if sufficient time has passed since the last fire so that white cedar seeds have become imbedded in the peat, a dense stand of white cedar reproduction springs up after burning. Removal of other vegetation and slash favors the white cedar seedlings under such conditions. If fire sweeps these swamps during the dry season, or close enough on a previous fire that no cedar seeds are stored, the change is to a forest of the associated species without cedar. A very severe dry season fire will eliminate the associated pines, leaving a stand of sprout hardwoods (88, 90).

Fire successions in these swamps are as follows:

Condition	Next stage(s) in succession
Fire during wet season, many years after previous fire	Pure stand of white cedar
Fire during wet season, a few years after previous fire, or moderate fire during dry season. In northern range of white cedar	Pure stand of pond pine

Above conditions, in southern range of white cedar	Pure stand of slash pine
Severe fire during dry season, in northern range of white cedar	Sprout stand of black gum

IV. UPLAND FORESTS

11. *Upland Mixed Pine and Oak Forests*

Rôle of fire in the origin of this forest. Due to scattered distribution of information, all upland pine-hardwood forests are best combined into one broad type for a discussion of fire effects.

Most of these mixed forests appear to have originated in the normal course of secondary succession—more rarely in primary succession—so that fire has not played an important rôle in the origin of this type. Sometimes, however, fire may bring about conversion of oak forests to types in which shortleaf pine (*Pinus echinata* Mill.) or loblolly pine (*P. taeda* L.) predominate (16, 127). On the other hand, bog areas in the coastal plain sometimes change to loblolly-mixed oak forests as a result of fire protection (162).

It is generally agreed that the loblolly-shortleaf-hardwood forests of the Southeast are fire sub-climaxes (16, 49, 127, 163). Released from fire they go to oak-hickory in normal succession.

Effects of fire on surviving plants and on species-composition of the upland mixed forest. Loblolly and shortleaf pines show considerable reduction in growth rate as a result of fire (10, 13). Diameter growth of shortleaf may decrease as much as 75% following one fire (33). When mature, these pines are less susceptible to fire scarring than associated hardwoods. Sometimes only half as many loblolly pines as oaks and only one-fourth as many pines as hickories show fire scars (41). In a burned area as many as 30% of the shortleaf pines may be fire wounded, but this species is still less susceptible than longleaf (20, 35).

An ordinary fire may kill all loblolly seedlings under five years old, a severe fire may kill seedlings considerably older (104, 114, 162). Thus annual burning effectively stops loblolly reproduction (7, 21, 137). Shortleaf pine is not so easily eliminated by fire, since up to 56% of the shortleaf seedlings may survive by sprouting, but this sprouting is not so consistent when shortleaf pines are over eight feet high (138, 160). In spite of sprouting, though, fire can eliminate or decrease shortleaf in a mixed forest (3, 33). Virginia pine (*P. virginiana* Mill.), a minor species, is so sensitive to fire that it is usually found only on areas escaping frequent

burning (61). Oak reproduction may also be decreased in these forests as a result of fire. Soil temperatures during an average fire are high enough to kill all acorns (89). Sprouting quickly offsets this effect (158).

Frequent burning of loblolly-hardwood areas, therefore, gradually eliminates loblolly and favors sprouting hardwoods (7). Loblolly-shortleaf-hardwood forests so treated change to shortleaf-hardwoods, but with continued burning the shortleaf is eliminated, leaving only sprout hardwoods (3). This change to hardwoods is particularly evident when cutting of pines is followed by fire (158).

These familiar sprouting scrub-hardwood areas of the Southeast are in striking contrast to the typical oak-hickory climax forest. Between frequent burning with its resultant scrub-hardwoods and almost complete protection with its resultant oak-hickory climax is the fire frequency which maintains the upland mixed forest as a fire sub-climax. Chapman (26) suggests that fires more often than every ten years may eliminate these pines, but just what frequency maintains the mixed type has not yet been suggested.⁴

Fire and fire-relief succession in the upland mixed forest.

Report	Conditions	Next stage(s) in succession
(General)	Almost complete fire protection	Oak-hickory—?→beech-maple
(26)	Fire, less often than ten-year intervals	No change. Mixed forest remains
(76)	No fire in upper coastal plain, well-drained soil	Pines, red oak, → pines, dogwood oaks
(76)	Same as above, but moister soil	Red, black gum → pine, gum
(114)	Fire following cutting in pine, hardwoods	Scrub oaks and other hardwoods
(84)		
(26)	Fire in mixed forest, more often than every ten years	Sprouting hardwoods

12. Upland Red Cedar-Hardwood Forest

According to Harper (55, 61, 65), local distribution of red cedar (*Juniperus virginiana* L.) is governed by fire. Thin bark and low

⁴ In a publication which appeared after this report had been completed (H. H. Chapman, Management of loblolly pine in the pine-hardwood region. ... Yale Univ., Sch. For., Bull. 49. 1942), the rôle of fires in eight to ten year frequencies in maintaining loblolly pine as a component of the mixed forest is discussed at length. The importance of fire in exposing the mineral soil essential to germination of loblolly pine seeds is stressed. Since oak sprouts over five years old and loblolly pines over eight years old are indicated as usually surviving winter fires, the rôle of fire in promoting loblolly pine must be threefold: a) furnishing bare soil for seed germination; b) eliminating competition of herbs and fast-growing hardwoods of the red gum type; c) eliminating oak sprouts under five years old. Other references expressing the same ideas are listed in this bulletin.

branches make it very susceptible to fire. This indicates that the scattered areas of mixed forest in which red cedar predominates are found only on stations escaping fire.

13. *Upland Scrub-Oak Forest*

As previously indicated, many of the extensive areas of scrub oaks in uplands of the Southeast have originated through continued burning of the mixed upland forest (20). The same is true in other regions (30, 87, 92). That these scrub oak forests are perpetuated by continued burning is also evident (87, 92).

Only a few references have been made to the effects of fire on the established scrub oak forest. In the Lake States burning kills almost all oak sprouts under four inches in diameter, thus permitting oaks to be replaced as dominants in the scrub forest (92). Soil loss through washing may be 12 times as great on annually burned scrub oak areas as on similar unburned areas, and water loss through runoff may be 31 times as great (38). As much as ten inches of soil may be lost per year under such burning (107). Forage grasses may decrease 40% to 60% on scrub oak types burned every year (38).

14. *Upland Oak-Hickory Forest*

Fire and the origin, soil and individual plants of the oak-hickory forest. Recency of cultivation makes pine so prominent in most southeastern forest areas that pure oak-hickory forest is rather rare. According to Haig (49), many ecologists believe that the oak-hickory forest of the prairie region is a fire sub-climax of beech-maple. In the Southeast, however, it is indicated that this forest is often a response to absence of fire (16, 49, 127, 163). In Arkansas oaks sometimes take over protected grazing areas, and it is probable that the sandhill scrub forest of North Carolina, if protected, will change to hickory or blackjack oak and then to oak-hickory (105, 165).

It is agreed that, due to leaching of ashes, the fertility of oak-hickory forests is depleted by burning (39, 85, 106, 116, 119). Runoff of water on such burned areas may be 130 times as great as on unburned areas, and the resultant soil eroded may be ten times as great (15). Likewise, the rate of water absorption and amount absorbed is greater for unburned oak-hickory soils (8, 9).

Mature black oaks (*Quercus velutina* Lam.), scarlet oaks (*Q. coccinea* Muench.) and dogwoods (*Cornus florida* L.) are readily injured by fire. White oaks (*Q. alba* L.) and chestnut oaks (*Q. montana* Willd.) are intermediate in resistance, and yellow poplar (*Liriodendron tulipifera* L.) and red maple (*Acer rubrum* L.) show high resistance to fire scarring (41, 112, 135, 143, 144). It has also been indicated that growth rate of trees is reduced on burned oak-hickory areas (119).

Effects of fire on species-composition and succession in oak-hickory forests. The number of young trees in this forest is appreciably reduced by fires. From 40% to 95% of one-inch oaks and hickories and 3% to 75% of the five-inch class may be killed by one fire (99). Large trees are much less susceptible. In the southern Appalachians the thick growth of fire-initiated sprout reproduction is low in yellow poplar, chestnut oak, red oak and white oak. The shift is towards scarlet oak, hickories, red maple, dogwood and sourwood (*Oxydendron arboreum* (L.) DC) (39, 127). A minor species, Kentucky coffee tree (*Gymnocladus dioica* (L.) Koch.), may sometimes be found in large numbers on some burned-over areas, since its seeds germinate much more readily when the seeded area is burned (82). White oak, in particular, reproduces poorly on burned-over land and it also does not regenerate readily by sprouts when exposed to frequent fires (26, 127). An average fire produces heat enough to kill all acorns on the forest floor, thereby reducing the number of oak seedlings (89).

It is evident that the first stage in fire succession in the pure oak-hickory forest is a sprout forest (20). Continued burning may eventually result in a vegetational type in which *Andropogon* is dominant (162). When shortleaf pines are scattered through the oak-hickory type fire succession may bring about a pure shortleaf pine forest (127).

V. NATURAL OR ARTIFICIAL NON-FORESTED AREAS

15. Southeastern Prairies

In the Southeast, scattered prairie regions are now found in Louisiana, Arkansas and the Louisiana Delta, and a few remnants remain of the original black-belt prairie of Alabama. Apparently, these prairie regions are not vegetationally related either to each other or to the western prairies (64).

An often-expressed belief that fire was responsible for the origin of the western prairies is much disputed (80). Apparently, fires are rare in the remnants of the Alabama prairie, since fire-susceptible species, such as red cedar and bluets (*Houstonia angustifolia* Michx.), abound there (64). It is also probable that not fire but poor drainage is effective in maintaining the Louisiana and Arkansas prairies (152). Some prairie regions in Kentucky, however, appear to have been originated and maintained through fire (132). Fire is also given partial credit for maintaining the Louisiana coastal prairie (117). There are, undoubtedly, southeastern fire-created artificial prairies, as are those in New York (56).

In succession the Louisiana coastal prairies, when fire is prevented, go directly to live-oak climax (117). The Kentucky prairies have been eliminated by fire prevention. The change was to blackjack oak, then to red oak, and lastly to oak-hickory climax (132).

16. Southeastern Coastal and Swamp Marshes

Little is known regarding the rôle of fire in the swamp marshes of the Southeast. It is frequently suggested that the Everglades may be a fire-maintained type. In these Everglades marshes—saw grass (*Mariscus jamaicensis* (Crantz.) Britton) and cabbage palm (*Sabal palmetto* (Walt.) Todd)—fire causes excessive lime to be formed in the soil (5, 30). The influence of this on the vegetation has not been studied.

In the coastal marshes of Louisiana, where saw grass and other species of the genera *Juncus*, *Scirpus*, *Carex*, *Arundinaria*, *Panicum* and *Typha* abound, natural succession is delayed by fire, and re-vegetation following burning is retarded because of excessive leaching of the ashes (118, 151). Lynch has correlated vegetational changes in these marshes with types of fires as follows (97, 98):

When the roots are protected by water, fire has little effect. Such burns promote growth of *Scirpus Olneyi* A. Gray and decrease growth of wire grass (*Spartinia patens* (Ait.) Muhl.), but this change is of short duration. Dry season fires which burn the roots kill off the typical plants of the various marsh types. Such plants as wire grass, saw grass and *Panicum hemitomon* Schult. are so destroyed. These are replaced, temporarily, by spike rush (*Eleocharis* sp.) and water lily (*Castalia* sp.), but the latter do not usually remain long and are soon replaced by new growth of the

typical marsh plants. Time required for replacement of these fire-succession types depends upon such factors as severity of burn, water level and number of rhizomes left. Burns which go deep into the peat produce pools in which water lilies and widgeon grass (*Ruppia maritima* L.) grow. Such pools may remain several decades but are eventually taken over by the original marsh.

17. Southeastern Grass-Sedge Bogs or "Savannahs"

From the point of view of variety of floral beauty few regions equal the open bog areas of the Southeast. These grass-sedge areas (*Campulosus-Panicum*, in general) are typical examples of a sub-climax maintained by fire (163, 164). Fire also appears to be responsible for the origin of most of these bog areas.

Wells (164) believes that many of these bogs are found on areas which would have gone to beech-maple climax without fire, but fire in past ages changed the succession to *Arundinaria-Ilex* bogs. The frequent fires of modern times have changed the *Arundinaria-Ilex* bogs to *Campulosus-Panicum* sub-climaxes. Sometimes pocosin areas are converted to "savannahs" by fire (161). Fire after cutting of longleaf pine on moist sandy flatwoods, and after cutting of Florida hammocks, also brings about establishment of "savannahs".

The following fire-relief successions for grass-sedge bogs have been indicated by Wells (162, 164, 165):

Condition	Next stage(s) in succession
Freed from fire after erosion	Pines→ <i>Ilex-Myrica</i> →Oak-hickory→Beech-maple
Freed from fire, no erosion having taken place	Pines→Oak-hickory→beech-maple

18. Southeastern Pastures

Burning-over of pastures has been a common practice in the Southeast for many years (22). Apparently, this burning is sometimes an important factor in maintaining pastures against normal old-field succession to pine (137, 141). It may also hasten establishment of grasses on old fields (18).

Burning of some Florida pastures causes a decrease in mineral matter and a loss of water from the soil (129). In Kansas pastures containing grasses also found in the Southeast, little change in soil mineral and organic matter results from fire (4). In general,

burning of broomsedge causes a temporary decrease in soil acidity (126).

Plants in Florida pastures show little or no growth if protected for a year, then burned after May; if protected for two years, then burned in March; or if protected for three years, then burned at any time (94). On new pasture areas continued burning may maintain annual grasses and prevent establishment of perennial grasses (18).

The effects of burning on the species-composition of pastures vary greatly from region to region. Burning of coarse grasses of various species known as "wire grasses" is reported as eliminating these grasses in Florida and increasing them in Arkansas (20, 94). In *Andropogon* pastures, apparently, burning either decreases or brings about no change in the weed composition (4, 70). Bluegrass in pastures may be either eliminated or increased by burning (4, 44, 142). Burning of improved southeastern pastures may eliminate introduced forage plants and favor growth of broomsedge (1). In general, the season during which the fire occurs has much to do with these effects on species-composition (4).

Grasses growing on burned areas show a greater concentration of phosphorus, potassium, iron, nitrogen and crude fiber during the early part of the season than grasses on unburned areas (94, 111). These differences become less evident as the season advances. There is a difference of opinion regarding calcium and magnesium concentration of grasses on burned and unburned areas (94, 111). Mineral composition of roots and crowns of grasses apparently is not influenced by burning (94).

SUMMARY

Fire is a very important factor in the plant ecology of the southeastern United States.

In reviewing the effects of fire, the nature of available information has made it necessary to combine the plant communities into 18 major vegetational types.

It is probable that the longleaf forest of the Southeast originated as a result of fire. It is undoubtedly a fire sub-climax type.

Summer fires or annual fires result in destruction or suppression of longleaf reproduction. Longleaf seedlings are also readily killed by fire at any time during their first year and during their sixth to eighth year period.

Frequent winter fires in the proper ratio to fire-free years appear to be essential to maintenance and perpetuation of this longleaf forest type. Such fires result in increased germination of longleaf seeds and promote the survival of longleaf seedlings through control of the brown-spot needle disease and through removal of competing vegetation.

Fire will kill all seeds and most roots within the upper inch of longleaf forest soils. Soil fauna is scarce in such frequently burned soils.

The soil of frequently burned longleaf forests show higher temperatures, lower soil moisture, more massive structure and less penetrability than comparable unburned soils.

Most evidence indicates that burning results in decreased acidity and increased nitrogen, replaceable calcium and organic matter in longleaf soils. Return of minerals in ashes and greater growth of legumes and other herbs on burned-over areas contribute to these changes. The past history of the soil seems to influence these changes so that exactly opposite results follow fire in longleaf forests on abandoned fields.

Frequent winter fires after the first year promote the growth of longleaf seedlings. Saplings, however, show decreased growth rates following fires. Gum yield is also reduced by fire. In both cases recovery is rapid.

Frequent winter fires remove other species of pines and hardwoods from the longleaf forest and thus are responsible for the familiar pure stands of longleaf pine.

Almost all fire-influenced succession in the longleaf forest is fire-relief succession. These successions are outlined for various soil types.

In the open range areas of the longleaf forest, burning appears to maintain or increase the herbage. Fire-influenced changes in species-composition of herbage are outlined.

Indirect evidence indicates that continued burning may be responsible for the southeastern longleaf-scrub oak forest. Steps are outlined whereby fire might bring about establishment of this forest type. Fire-relief succession for this forest type is also outlined.

Slash pine seems to be less sensitive to fire than most hardwoods, and more sensitive to fire than longleaf pine. Thus the slash pine

forest of southern Florida must have originated on areas where hardwoods were destroyed by fire, while the slash pine forests of the longleaf belt originated as a result of invasion of protected longleaf areas by the faster growing slash pine.

Frequent fires in a slash pine forest will eliminate slash pine, since its germination, survival and permanent establishment are hindered by fire. Growth of older slash pine is retarded by fire.

Definite trends in fire and fire-relief succession are outlined for the slash pine forest.

It is possible but doubtful that the sand pine-scrub oak forest originated as a result of fire. In this forest fires result in an increase in sand pine if the pines are old enough to bear cones. Otherwise, fire destroys the pines, leaving scrub oak barrens.

Little is known regarding the rôle of fire in coastal plain bottom-land hardwoods.

Evidence indicates that fire is always involved in the origin and perpetuation of the coastal plain scrub oak forest. Fire-relief successions are outlined for this forest.

There is no agreement as to whether or not the southeastern hammocks originated only on protected areas. Fire readily destroys these hammocks.

The southeastern pocosins appear to be due to a combination of poor drainage, fluctuating water table and infrequent fires. Fire-influenced successions are outlined for the pocosins.

The rôle of fire in southeastern cypress swamps is unsettled.

The results of fire in southern white cedar swamps vary from complete eradication of the white cedar to a dense stand of pure white cedar, depending upon the season of burning, and time elapsed since the last fire.

Fire does not seem to be directly connected with the origin of the upland mixed forest, but this forest is regarded as a fire sub-climax type. Definite changes in species-composition and fire and fire-relief succession are outlined for this forest.

The upland red cedar-hardwood forest is found only on areas escaping fire.

Upland scrub oak forests have originated through continued burning of the upland mixed forest. Much soil erosion results from fire in this type.

Apparently, the southeastern oak-hickory forest is found only

where fires are very infrequent. Fire in this forest decreases soil fertility, increases erosion and promotes definite changes in species-composition.

Southeastern prairies, as a rule, do not appear to be fire sub-climax types.

In southeastern coastal marshes definite changes in vegetation result from fire. These changes vary with the season of burning.

The southeastern grass-sedge bogs are definite fire sub-climaxes. Protected from fire they change to forest areas.

The evidence regarding effects of fire in southeastern pastures varies so greatly that no definite general conclusions can be reached.

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Articles received and awaiting publication

Lichens—Their Biological and Economic Significance	G. A. PEREZ-LLANO <i>Harvard University</i>
Root-rots of Some Non-cereal Crops	G. H. BERKELEY <i>Dominion Laboratory of Plant Pathology</i>
Recent Developments in the Classification of Bacterial Plant Pathogens	CHARLOTTE ELLIOTT <i>Bureau of Plant Industry</i>
Phytogeography of Patagonia	A. A. BEETLE <i>University of California</i>
The Classification of Inflorescences	H. W. RICKETT <i>New York Botanical Garden</i>
The Inferior Ovary	GERTRUDE E. DOUGLAS <i>New York State College for Teachers</i>
Control of Noxious Plants	H. K. WILSON <i>University of Minnesota</i>
Classification of the Green Algae	F. E. FRITSCH <i>University of London</i>

Articles arranged for most recently

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The Male Gametophyte of Angiosperms	A. GERSHOF <i>University of Vermont</i>
Techniques for Aseptic Growth of Plants	L. C. KNORR <i>Cornell University</i>
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Articles in course of preparation

The Cytology of Fertilization in Angiosperms	L. E. ANDERSON <i>Duke University</i>
Development of the Madre-Tertiary Flora	D. I. AXELROD <i>University of California</i>
Relation of Wood Anatomy to Taxonomy	I. W. BAILEY <i>Harvard University</i>
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